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Deep-Sea Research II 51 (2004) 1289–1300

DEEP-SEA RESEARCH
PART II

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A comparison of net and acoustic estimates of krill density in the Scotia Sea during the CCAMLR 2000 Survey

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Accepted 18 June 2004
Available online 30 September 2004

Abstract

A multi-ship, multi-national survey to assess the acoustic biomass of Antarctic krill across the Scotia Sea was undertaken in January and February 2000. In addition, a total of 135 Rectangular Midwater Trawls (RMT8) were undertaken to determine the structure of the krill population and to validate acoustic target detection techniques. This paper reports a comparison of the density estimates derived from net and acoustic sampling for a range of spatial scales; from individual net hauls to regional estimates of krill biomass. The different sources of error and the different characteristics of the density estimates from net and acoustic techniques are also defined. Direct quantitative comparisons of net and acoustic densities are shown to be inappropriate at both the small scale (i.e. individual net tows; the typical net sampling unit for census surveys) and the large scale (i.e. regional surveys). Therefore, a direct comparison of density estimates from net and acoustic surveys is not practicable for retrospective analysis of krill abundance. However, the results of net and acoustic surveys do appear comparable in terms of trends in krill distribution at the large scale. Therefore, the combined use of net and acoustic data can be useful in the analysis of interannual trends in the variability of krill distribution at the regional level. At the local level, data from trawl surveys using comparable nets can be used to examine interannual variability in krill distribution as there has been little change in the methodology used for net surveys over the last 25 years.

1. Introduction

Antarctic krill, *Euphausia superba* Dana, is a key organism in the Southern Ocean food web and an important species for commercial fisheries in

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doi:10.1016/j.dsr2.2004.06.005

Antarctic waters. An understanding of the spatial and temporal variability in krill distribution (in terms of both interannual and interseasonal variability) and reliable monitoring of krill stocks are essential for the management of krill stocks using the ecosystem approach adopted by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (CCAMLR, 1993, 2000; Hewitt and Linen Low, 2000; Miller, 2002).

Extensive information on krill distribution has been accumulated during national and international programs undertaken in the Southern Ocean over the last hundred years. Until the 1980s, the data were mainly derived from net or trawl surveys. Acoustic survey techniques developed rapidly during the 1980s, and since the early 1990s acoustic surveys have become the main method for quantitative assessments of krill biomass. Nevertheless, net sampling is still an important component of acoustic surveys; acoustic sampling generates estimates of krill biomass and distribution, while net samples are used to provide krill length–frequency data for target strength estimation, to describe krill demography, and to study the occurrence of major zooplankton taxa (Siegel et al., 2000; Watkins, 2000).

To date, the major long-term time series data sets of krill abundance in the Southern Ocean comprise mesoscale estimates derived from either net-based or acoustic-based surveys. For example, the Elephant Island area (Antarctic Peninsula) data sets compiled by Siegel et al. (1997) are based on net estimates (1977–1994) while those compiled by Hewitt and Demer (1994) are based on acoustic estimates (1981–1993). Multi-year data sets that characterize krill distribution within much larger areas, such as across the entire Scotia Sea, are of special significance. Since 1981, five large-scale surveys have been undertaken within the Scotia Sea region: three trawl surveys (undertaken in 1983/1984, 1984/1985, and 1987/1988—Sushin and Shulgovsky, 1999; Sushin et al., 2001) and two acoustic surveys (1981—Trathan and Everson, 1994; and 2000—Trathan et al., 2001).

A direct comparison of such surveys would be of great value in assessing whether large-scale changes in krill biomass and distribution had occurred since the early 1980s. However, before this can be attempted it is first necessary to assess the comparability of net and acoustic estimates of krill abundance.

This paper reports on whether trawl surveys can be used together with acoustic surveys to compare spatial and temporal variability in krill distribution and abundance. This is achieved by comparing krill density estimates from net samples with the acoustic samples recorded during the corresponding hauls. The paper also reports on the comparability of large-scale distribution patterns and abundance estimates and assesses the likelihood of fishing tactics affecting the correlation between the density estimates from trawl and acoustic surveys.

2. Materials and methods

The net and acoustic data used here were obtained during a large-scale multinational, multi-ship survey of krill biomass within Area 48; the key fishery and management area that extends through the Scotia Sea and Antarctic Peninsula region of the Southern Ocean. This was sponsored by the CCAMLR and took place during January and February 2000. Full details of the CCAMLR, 2000 Survey are reported by Watkins et al. (2004).

2.1. Net sampling

Each of the four survey vessels taking part in the CCAMLR, 2000 Survey used a Rectangular Midwater Trawl (RMT8 + 1). The RMT8 + 1 was considered the most appropriate of the nets presently used for sampling krill owing to its widespread availability and frequent use in other surveys (Siegel et al., 2004). During the survey period, the four vessels sampled 135 net stations, which included 16 targeted tows and 119 standard double oblique net tows.

The standard double oblique net tows were carried out according to a standard protocol on each of the four vessels and formed a core biological data set. The night-time net stations were carried out around local midnight and the midday stations shortly before noon. The net was fished to 200 m (or to within 10 m of the bottom at stations shallower than 200 m) at a constant rate of $0.3\,\mathrm{m\,s^{-1}}$. This depth range was selected by combining the acceptable trawl duration and the potential vertical depth of krill (Siegel et al., 2000). The vessel's speed during hauling was 2.5 ± 0.5 knots. A flow meter and a real-time depth recorder were attached to determine the volume of water filtered and the net trajectory.

Targeted net hauls were undertaken to reduce the uncertainty associated with delineating acoustic backscatter attributed to krill (Watkins and Brierley, 2002). The depth and duration of the targeted hauls varied according to the nature of the targets. Krill net density at each station was estimated from the weight of krill in the catch and the volume of water filtered. These density estimates were then compared with those calculated from the acoustic sampling. Further details of the net sampling programme, and the data recording and analysis are described by Siegel et al. (2004).

2.2. Acoustic sampling

The acoustic data were collected on each of the four ships using a Simrad EK500 echosounder with 38, 120, and 200 kHz hull-mounted transducers and SonarData's EchoLog_EK data logging software in accordance with predetermined acoustic sampling protocols (further details are provided by Hewitt et al., 2004; Watkins et al., 2004). Standard sphere calibrations were conducted on each vessel before and after the CCAMLR, 2000 Survey (CCAMLR, 2000; Hewitt et al., 2002, 2004).

Post-processing of multi-frequency echosounder data sets was carried out using SonarData's EchoView post-processing software using the techniques developed at a CCAMLR workshop (CCAMLR, 2000; Hewitt et al., 2004). Acoustic backscatter was attributed to krill when the difference between mean volume backscattering at 120 and 38 kHz was greater than 2 dB but less than 16 dB (Watkins and Brierley, 2002). For double oblique hauls, 120 kHz acoustic backscatter attributed to krill was integrated from a surface exclusion line (at around 20 m) to 200 m and averaged over a horizontal distance of 100 m. For targeted tows, 120 kHz acoustic backscatter attributed to krill was only integrated within the depth layer fished by the net. Integrated backscattering area was converted to areal krill biomass density by applying the conversion factor equal to the quotient of the weight of an individual krill and its backscattering cross-sectional area summed over the length–frequency distribution (Hewitt et al., 2004). The conversion factors used for processing the CCAMLR 2000 Survey data (Hewitt et al., 2002; Siegel et al., 2004) have been applied in this paper.

Mean areal krill biomass density, $\bar{\rho}_s\,(\mathrm{g\,m^{-2}})$, and its coefficient of variation were estimated for each haul by averaging the density, ρ_s, obtained over each 100 m horizontal distance. An estimate of mean volume biomass density, $\bar{\rho}_v\,(\mathrm{g\,m^{-3}})$, was then calculated, representing the ratio of mean areal krill biomass density to the depth of the integration layer (such that $\bar{\rho}_v = \bar{\rho}_s/\text{integration depth}$). To investigate fine-scale vertical and horizontal spatial variability in krill distribution, a second estimate of mean volume biomass density, $\bar{\rho}_{vs}$ and its coefficient of variation, was derived by averaging the density ρ_{vs} obtained from each integration cell (100 m horizontal distance and 2 m depth) within the fished depth range during hauling. The dimensions of the integration cells were chosen with regard to the mean dimensions (length and depth) of krill aggregations within the Scotia Sea calculated from previous large-scale surveys (Miller et al., 1993; Siegel and Kalinowski, 1994). The vertical extent of the integration cell corresponds to the size of the vertical opening of the RMT8 trawl.

Acoustic estimates of krill density obtained for every nautical mile of transects traversed by the four research vessels were used to compare krill density estimates and krill distribution within the entire survey area. The mean values and 95% confidence intervals for the two techniques were obtained using a 'bootstrap' procedure (Efron, 1982). Horizontal and vertical distribution of krill biomass density was mapped using SURFER version 7 software.

3. Results

This paper focuses on standard double oblique tows because they formed the core biological data set for the CCAMLR, 2000 Survey. These data will also be important for comparisons with other surveys as standard double oblique tows are used during most trawl and acoustic surveys.

3.1. Net and acoustic density

A comparison of net and acoustic biomass density estimates based on the data from 119 standard double oblique net tows shows a significant difference between the frequency distributions obtained by the two techniques (Fig. 1A; Kolmogorov–Smirnov test, $P<0.05$). In particular, the proportion of zero-density estimates in the net sampling data is much greater than that obtained from the acoustic data.

A comparison of the two sets of krill density estimates for night and day stations only, reveals statistically significant differences between net and acoustic frequency plots (Figs. 1B and C). There is no correlation between net and acoustic density estimates (Figs. 1B and C; $r<-0.1$). In contrast to the situation for the standard double oblique net tows, acoustic and net density estimates for daytime targeted tows were highly correlated (Fig. 2; $r=0.93$).

A different relationship for the daytime and night-time net and acoustic density frequency distributions (Fig. 1) is clearly illustrated by the mean density estimates and their coefficients of variation (Table 1). Values of overall mean net density for the 119 standard oblique net tows (i.e. night plus day tows) or for the night tows only, were significantly higher than the respective values of overall mean acoustic density ($P<0.05$). In contrast, the mean acoustic density during the day was more than three times higher than the daytime mean net density. There was an almost five-fold difference between night and day net density estimates, in contrast to a two-fold difference between the corresponding values for acoustic estimates.

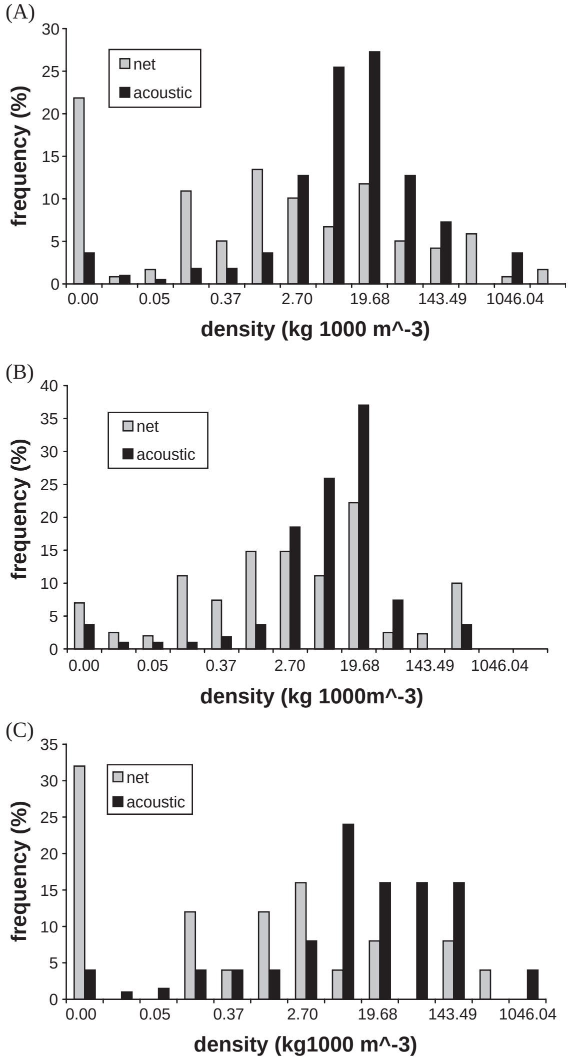

Fig. 1. Density distributions for net and acoustic samples. A standard double oblique tow was conducted at each station. Data are logarithmically transformed and illustrate: (a) day plus night stations; (b) night stations only; (c) day stations only.

3.2. Spatial distribution patterns from acoustic sampling

Echograms showed that during the standard double oblique net tows, net samples and acoustic observations were made of all the different types of krill aggregation described in the classification scheme of Miller and Hampton (1989), with the

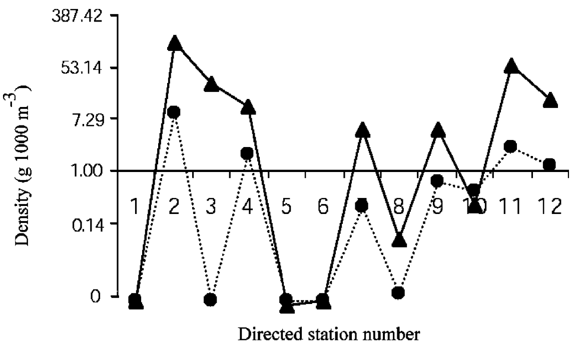

Fig. 2. Comparison of net and acoustic density estimates for targeted net tows. Data are logarithmically transformed. Zero density is represented by a value of −5.

Table 1
Density estimates obtained during standard double oblique net tows

	Net density		Acoustic density	
	Mean (g 1000 m^{-3})	CV (%)	Mean (g 1000 m^{-3})	CV (%)
Day plus night	60.608	3.842	44.350	3.423
Day	18.044	2.753	63.791	3.113
Night	98.613	3.192	26.349	3.417

exception of super swarms. This paper uses the two coefficients of variation of mean volume biomass described in Section 2.2 to investigate the spatial distribution of krill.

The coefficient of variation of mean volume krill biomass density, CV $\bar{\rho}_v$, characterizes the 100 m scale horizontal variation in the spatial distribution of krill. Thus, the lowest values of CV $\bar{\rho}_v$ were usually observed with the horizontally extensive layers or scattered forms of krill aggregations (Table 2; examples 28 (0.38), 51 (0.39), 53 (0.35)), while the highest values (e.g., Table 2; example 1 (5.68)) occurred when fishing swarms and irregular forms with restricted horizontal extent.

In contrast, the coefficient of variation of mean volume krill biomass density, CV $\bar{\rho}_{vs}$, characterizes both horizontal and vertical variation in the small-scale spatial distribution of krill. In this case, very high values of CV $\bar{\rho}_{vs}$ (max = 26.36) confirmed the restricted vertical distribution of the types of krill aggregation observed during the net hauls.

3.3. Comparison of net and acoustic density estimates in relation to patterns of spatial distribution

Uniform layers and scattered, dispersed krill aggregations are characterized by relatively low coefficients of variation (CV $\bar{\rho}_v$), and have a horizontal extent comparable to the horizontal distance covered by the net during a haul. When sampling such aggregations, the correlation between net and acoustic density estimates reaches a value of $r = 0.5$, and with acoustic density greater than net density. Similar ratios are observed during both day and night tows (Table 2; examples 6, 23, 28, 51, 53, 54) (Fig. 3).

The smaller, discrete swarms of krill are characterized by a relatively high value of CV $\bar{\rho}_v$. When fishing such swarms, the ratio of acoustic density to net density is extremely variable; the magnitude of the ratio is of a random nature. Thus, high acoustic density estimates may occur at very low net density estimates (Fig. 4) and vice versa (Table 2, examples 42, 56). A wide range of acoustic density estimates is found with zero net catches (Table 2). The acoustic density distribution pattern corresponding to a station with zero net catch and average acoustic density ($\bar{\rho}_v = 32$ g 1000 m^{-3}) is shown in Fig. 5. These examples demonstrate that with significant non-uniformity in krill biomass distribution within a fished depth layer, the catch size depends to a large extent on the net trajectory relative to 'patchy' spatial density distribution patterns. When the net encounters a swarm or enters the most dense parts of a layer, a large catch can be expected even if the krill biomass averaged over a 200-m fished depth range is low. In contrast, with high acoustic-density estimates characterized by a high coefficient of variation, unexpectedly, very low net densities may be observed (such as examples 1, 4, 9); sometimes more than 200 times lower than the respective acoustic-density estimates (Fig. 4). It should be noted that even during a targeted tow the pattern of krill distribution influences the catch; zero catches were observed when fishing

Table 2
Examples of net and acoustic density estimates based on data obtained simultaneously during day and night

Example	Day(D)/night(N)	Net density (g $1000\,m^{-3}$)	Acoustic density ($\bar{\rho}_v$ g $1000\,m^{-3}$)	
			Mean	CV
1	D	0.51	154.89	5.68
2	D	67.91	80.22	3.07
3	D	129.65	88.86	1.79
4	D	9.20	104.84	4.07
5	D	0.27	8.15	0.43
6	D	2.21	5.82	0.92
7	D	213.38	304.13	2.92
8	D	0.06	18.59	2.12
9	D	0.00	146.74	4.20
10	D	0.00	7.93	0.46
11	D	0.00	3.32	0.76
12	D	0.00	3.59	0.66
13	D	3.13	2.17	1.29
14	D	1.13	8.53	1.79
15	D	1.32	11.20	0.97
16	D	0.00	20.90	1.49
17	D	1.89	0.00	0.00
18	D	0.00	2.86	2.21
19	D	0.00	3.13	3.11
20	D	0.48	1.20	1.11
21	D	0.08	5.19	1.28
22	D	1.84	999.37	3.55
23	D	0.12	0.82	1.30
24	D	0.00	32.00	0.54
25	D	18.14	92.90	3.13
26	D	0.00	37.20	1.60
27	D	0.00	12.10	0.52
28	N	0.87	4.78	0.38
29	N	11.44	2.85	0.30
30	N	9.04	2.66	1.52
31	N	0.28	4.11	1.22
32	N	0.10	8.59	1.18
33	N	0.12	2.77	0.45
34	N	1628.19	5.10	0.27
35	N	5.46	8.91	2.55
36	N	1.02	8.53	0.49
37	N	8.29	3.04	2.21
38	N	0.17	0.76	0.71
39	N	0.48	16.14	0.22
40	N	193.19	2.01	0.85
41	N	253.61	3.53	0.72
42	N	187.48	1.96	0.36
43	N	397.92	8.33	2.23
44	N	6.95	0.51	0.73
45	N	1.52	6.86	0.42
46	N	11.5	1.61	2.34
47	N	5.03	1.85	0.68
48	N	15.9	48.92	3.86
49	N	1.19	474.00	2.09
50	N	0.49	11.86	1.94
51	N	1.42	17.27	0.39
52	N	0.00	0.00	0.00
53	N	0.70	9.95	0.35
54	N	0.10	15.90	1.07
55	N	18.72	3.27	1.10
56	N	301.57	4.1	1.90

groups of small, discrete swarms (Fig. 2). As Table 2 shows, the highest net density (1628.19 g $1000\,m^{-3}$) was obtained from a night haul. The corresponding mean acoustic-density estimate (5.10 g $1000\,m^{-3}$) and its coefficient of variation were not high. The spatial distribution pattern (Fig. 6) shows that krill aggregations necessary for such a high net density were not visible within the depth layer sampled by the hull-mounted transducer (i.e., between ~6 and 200 m). This suggests that surface krill aggregations were fished, i.e. those distributed above 5 m depth and which are thus not detectable by hull-mounted transducers. The other high night-time net densities also were accompanied by much lower estimates of acoustic density (Table 2; examples 40–43, 56), which contrasts strongly with the few high daytime net densities which always corresponded with high estimates of acoustic density (Table 2, examples 2, 3, 7).

3.4. Spatial variability of krill density in the CCAMLR 2000 survey area

Mean density estimates for the Scotia Sea were calculated from the net data and acoustic data. A comparison of the two data sets shows that mean net densities were generally less than the corresponding acoustic values, while the standard errors for the mean net densities were several times higher than those for the mean acoustic estimates (Table 3). Despite major differences between the net and acoustic sampling techniques, particularly in terms of the number and volume of

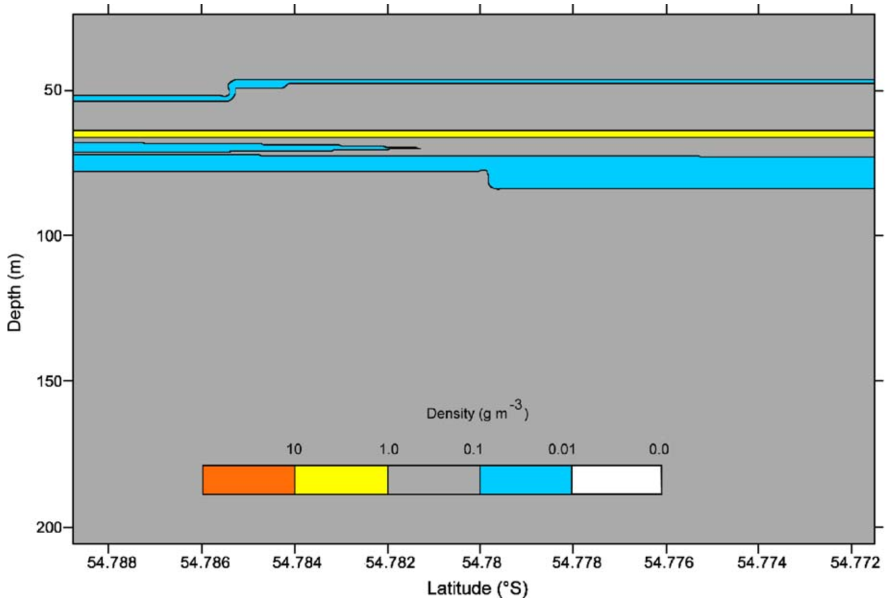

Fig. 3. Contour plot of vertical krill biomass distribution for a dispersed aggregation (e.g., a layer) (Table 2, example 51).

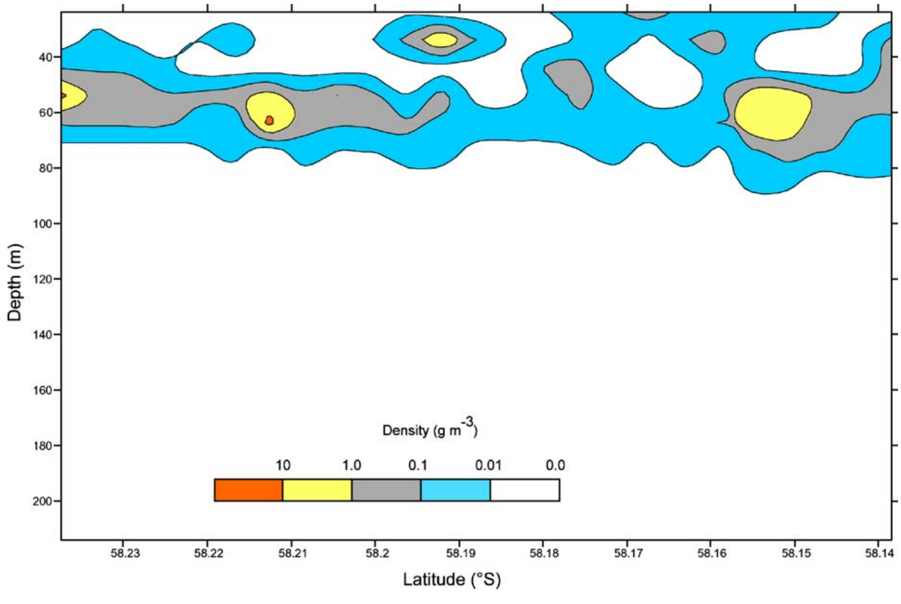

Fig. 4. Contour plot of vertical krill biomass distribution at a station with a low net catch (1.84 g $1000\,m^{-3}$) and a high mean acoustic density (999.37 g $1000\,m^{-3}$) (Table 2, example 22).

individual samples, there was a general similarity in the pattern of krill distribution using the two techniques (Fig. 7). However, the continuous along-transect coverage of acoustic samples can be used to produce a more detailed picture of krill biomass distribution.

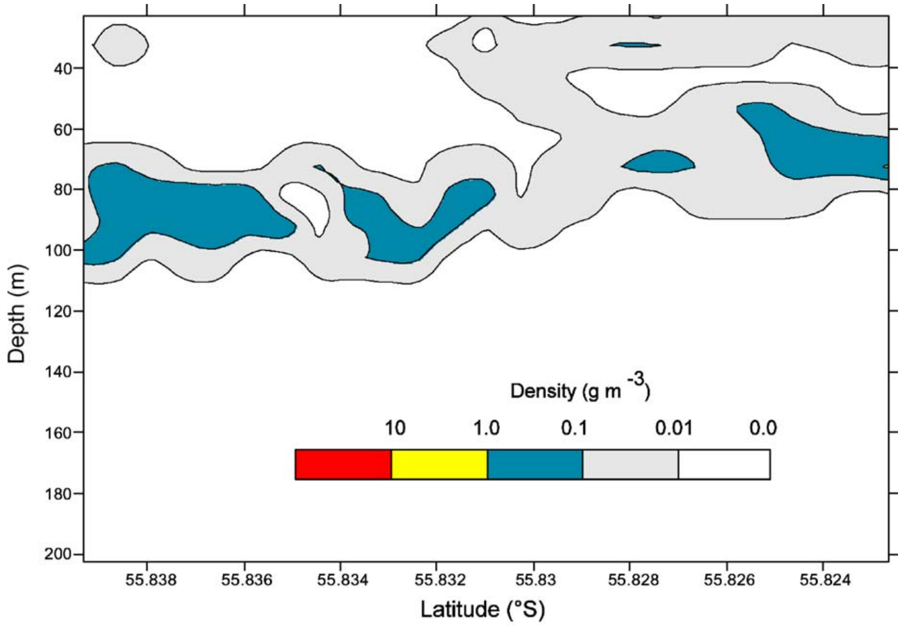

Fig. 5. Contour plot of vertical krill biomass distribution at a station with a zero net catch and a mean acoustic density of 32 g 1000 m^{-3} (Table 2, example 24).

4. Discussion

A comparison of krill densities derived from concurrent net and acoustic sampling shows substantial differences between the two sets of data, and a significant lack of correlation frequently occurs. Analysis of within-haul acoustic density for both night and day acoustic samples shows strong small-scale heterogeneity in the horizontal and vertical spatial distribution patterns of krill biomass. Such small-scale non-uniformity of krill biomass distribution is one of the major reasons for the difference observed between net and acoustic density estimates. A similar lack of correlation between net and acoustic density estimates was noted by Pauly et al. (1997) in a survey of the Indian Ocean sector of the Southern Ocean.

In contrast, the correlation observed between net and acoustic density estimates obtained during targeted net tows is generally better (this study; also Pauly et al., 1997; Watkins and Brierley, 2002; Watkins and Murray, 1998). However, the pattern of fished aggregations is of importance even in this

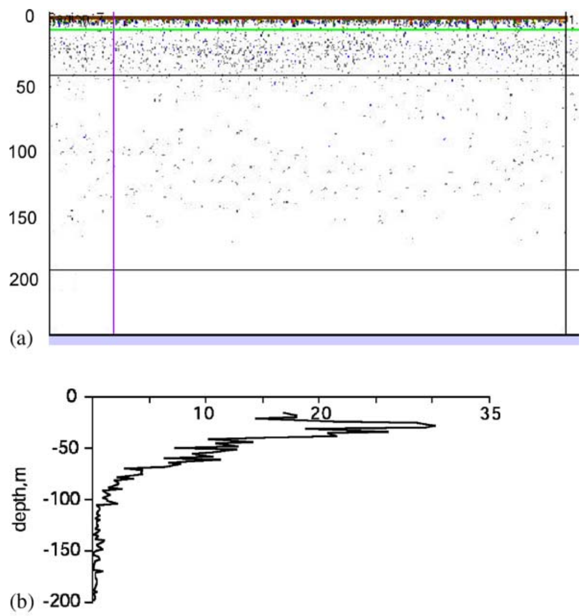

Fig. 6. Acoustic density distribution of krill over upper 200 m depth layer (excluding the upper 10 m) at a station with a high net density (1628.19 g 1000 m^{-3}) and a low mean acoustic density (5.10 g 1000 m^{-3}) (Table 2, example 13). (a) Acoustic echo chart for the trawl track. (b) Vertical distribution of krill acoustic density.

Table 3
A comparison of overall mean krill density estimates and their variability calculated using the 'Bootstrap' procedure. The acoustic density estimates are based on acoustic samples over 1 nm horizontal distance. Net density estimates were obtained from standard double oblique net tows

Stratum	Net samples				Acoustic survey			
	Mean density ($g\,m^{-2}$)	Standard error	Lower CI	Upper CI	Mean density ($g\,m^{-2}$)	Standard error	Lower CI	Upper CI
All strata	12.7	4.6	5.9	21.5	24.2	1.6	21.8	27.4
48.1, 48.2, 48.3	10.5	4.8	5.3	24.2	25.3	1.4	22.5	28.1
48.3	5.8	2.9	3.1	17.5	3.65	0.9	2.57	5.99
48.4	8.3	3.8	6.1	21.8	14.2	1.3	13.3	18.1

Lower CI and Upper CI-boundary of the 95% confidence interval.

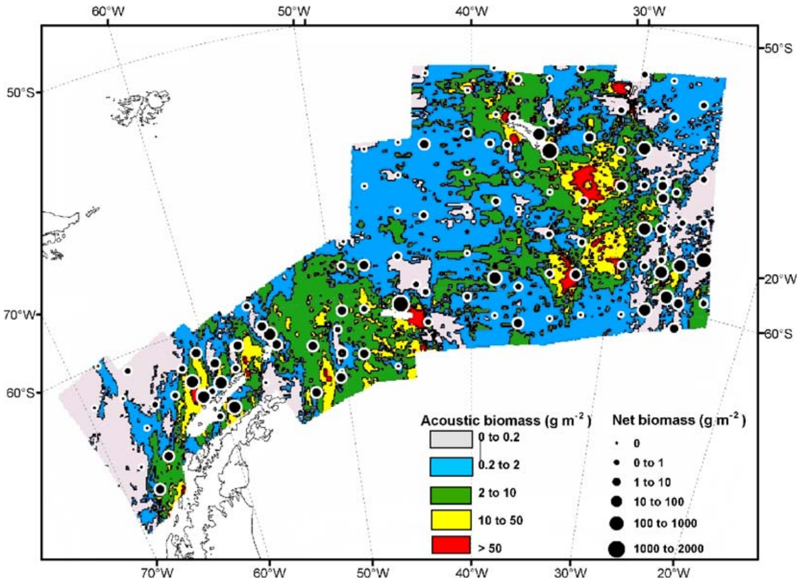

Fig. 7. Horizontal distribution of krill density. (a) Net haul density estimates from the standard double oblique net tows undertaken during the CCAMLR, 2000 Survey. (b) Acoustic krill density derived from the daytime survey.

case, and targeting a relatively small net at small, dense krill swarms is not always successful and in the present survey, some targeted hauls caught no krill.

If both the net and acoustic systems are considered as sampling a vertical slice of water with a nominal width in the third dimension of 1 m, then the area of water sampled by an RMT8 net (mouth area $8\,m^2$, vertical opening 2.5 m) in a typical double oblique net haul of 30 min duration is about $5800\,m^2$ at most, which is just 1.3% of the total area from the surface to the lowest level reached by the net (nearly 200 m vertical by 2300 m horizontal is $460{,}000\,m^2$). In contrast, the vertical area of water sampled acoustically during a typical net haul is 97.5% of the total potential sampling area. Therefore, with such a small area sampled by the net, the ratio of the vertical area actually occupied by krill to total potential sampling area of the depth range over which krill can occur, is significant. Thus, the chance of hitting a small, high-density swarm (which takes up little area in the water) is low. As demonstrated here, net sampling efficiency improves with the increasing size of krill aggregations, such as when fishing extensive dispersed aggregations or layers at night. The present results show that the density estimates obtained from double oblique tows are very susceptible to the non-uniform spatial distribution of krill. The actual net densities obtained are as dependent on the scale of patchiness of the krill aggregations as on the overall krill biomass present in the sampled water column. Therefore, net density values estimated with such a net are rarely representative of the total krill biomass present within the water column during a typical net haul.

Net and acoustic density estimates obtained during targeted net tows were highly correlated, in part, due to the comparable volumes of water sampled in such hauls. However, even in this case the net and acoustic density estimates were often quite different in terms of magnitude.

No net is able to catch all the krill in a population, and the catchability of the net is dependent on the availability of the krill to the net sampling and on the selectivity of the net (Table 4; Kasatkina, 1991). It has been shown that krill avoid small research trawls and that this manifests itself in various ways during the day and night (Everson and Bone, 1986). The extent of the vertical opening of an RMT8 net is no more than 3 m, while krill can attain escape velocities of more than $0.6\,\mathrm{m\,s^{-1}}$ (Kils, 1981). Everson and Bone (1986) observed that krill could easily avoid the net, suggesting that they move 10 m away from the trawl in 8 s.

Acoustic sampling covers the water column below the ship and is relatively unaffected by the non-uniform spatial distribution of krill. However, krill aggregations at depths shallower than 5–10 m are undetectable by standard hull-mounted echo-sounders. Miller and Hampton (1989) estimated that at night, nearly 40% of the total krill biomass may be concentrated at depths less than 5 m. In the CCAMLR, 2000 Survey, the overall mean night net density was more than three and a half times higher than the overall mean night acoustic density, and the highest net densities occurred with low acoustic densities (Table 2), thus suggesting that significant densities of krill were found very close to the surface at night. Such results confirm the importance of a major element of the CCAMLR, 2000 Survey design—only daytime acoustic surveys having been undertaken—which thus eliminated the possibility of underestimating krill biomass due to the formation of surface aggregations.

While acoustic surveys are less prone to not detecting krill, there are a number of likely errors

Table 4
Comparison of sources of error for density estimates obtained from net and acoustic sampling (Watkins, 2000)

	Net sampling	Acoustic sampling
Species identification	Reliable	Dependent on accuracy of algorithm of multi-frequency method used for acoustic identification
Availability of krill		Biased if krill at surface
Net avoidance	Problem, although reduced at night	Not applicable
Net catchability	Problem. Catchability of net dependent on spatial distribution patterns of krill aggregations fished	
Sampling volume	Very low	Very high
Heterogeneity of krill distribution	Marked effect on reliability of estimate especially in relation to sampling volume	No effect on biomass estimate
Diel changes in behavior of krill	Improved biomass estimates if krill more dispersed	Changes in tilt angle of krill orientation could have large effect on target strength and biomass estimates

and biases that may affect the estimated biomass. Such errors are most probably related to uncertainties in species delineation and target strength (Demer, 1994, 2004; Maclennan and Simmonds, 1992). Under the conditions found during the CCAMLR, 2000 Survey, there was a significant correlation between net and acoustic estimates of density for targeted net tows, confirming the suitability of the two-frequency difference algorithm to delineate krill from other scattering organisms (Watkins and Brierley, 2002). A major effect of target strength on uncertainties in density estimates is generally related to animal behavior: diel changes in animal orientation may cause a substantial difference between forecasted magnitudes of target strength and real values (Demer, 1994; Everson, 1982). Demer (2004) provides a full analysis of the combined errors and biases of the acoustic biomass estimates from the daytime surveys.

Thus, the availability of krill and the errors associated with net and acoustic density estimates are very different (Table 4). Therefore, direct comparison of net and acoustic density estimates at the scale of the individual double oblique net tows (i.e. at the typical net sampling unit for census surveys) is not feasible.

At the scale of an entire survey, the main trends observed in variability and horizontal distribution derived from net samples are not dissimilar to those derived from the acoustic surveys. This level of comparability of net and acoustic density samples in terms of patterns and trends arises mainly from the effect of combining large numbers of sampling units. Nevertheless, owing to the smaller sample size, the mean net densities are likely to be characterized by a higher standard error and a larger confidence interval than those arising from acoustic sampling. Furthermore, there is a considerable discrepancy between the regional stratum mean densities observed from acoustic and net samples (Table 3) and the estimates obtained by the two techniques are not comparable in absolute terms even at the large scale.

The present study indicates that net and acoustic density estimates are non-comparable in terms of absolute value both at the small scale (individual net sampling unit) and at the large scale (at the scale of survey areas). The results of net and acoustic surveys are only comparable in terms of trends in krill distribution at the large scale. This has several implications in surveys used to estimate the biomass and distribution of krill: (1) long-term patterns in krill distribution can be compared by combining data sets based on either net-based or acoustic-based surveys; (2) biomass estimates based on data from net and acoustic surveys should not be compared given the different errors associated with each type of survey (only very large changes in biomass are likely to be detected using this approach); (3) the technologies of net surveys have not undergone noticeable change during the last 25 years, so such surveys form a solid basis for long-term monitoring of changes in krill distribution and abundance. These conclusions imply that a sufficient level of net sampling should be maintained on future acoustic surveys to enable calculations of both net-based and acoustic-based estimates of biomass.

Acknowledgements

We thank the officers and crew of the R.V. *Atlantida*, R.R.S. *James Clark Ross*, R.V. *Kaiyo Maru*, and R.V. *Yuzhmorgeologiya* for their help in conducting the survey and net sampling. We thank all colleagues who worked on the ships to collect the acoustic and net data sets; in particular, we acknowledge the significant effort of Drs Kawaguchi, Loeb, and Siegel for overseeing the net sampling programs. We thank the two anonymous referees for their comments which have improved this manuscript.

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